

The new fossil genus of Vianaididae (Heteroptera: Tingioidea) from the Cretaceous amber of New Jersey; evolution of the family in the Late Cretaceous

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Abstract. A new genus and species *Vianathauma pericarti* gen. et sp. n. (Heteroptera, Vianaididae) is described from the amber of New Jersey (Upper Cretaceous, North America). It is the second known fossil monotype genus of the family alongside with two modern genera that have been described so far. Earlier presented synapomorphies for Vianaididae and Tingidae, as well as autapomorphies for Vianaididae are also specified. Taking fossil genera *Vianagramma* GOLUB & POPOV and *Vianathauma*, n. gen. as an example, authors propose two directions of morphological differentiation of Mesozoic Vianaididae. In the Cenozoic, one of these directions caused formation of specific coleopteroid myrmecophilous forms with punctate but no areolate hemelytra.

Key words: Heteroptera, Tingioidea, Vianaididae, *Vianathauma pericarti*, new genus, new species, New Jersey amber, Upper Cretaceous.

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I. INTRODUCTION

This small Neotropical cimicomorphan tingoid group was described as a separate family Vianaididae by KORMILEV (1955). He was right to relate it to the family Tingidae, although later on some authors treated it only as subfamily (DRAKE & DAVIS 1960; DRAKE & RUHOFF 1965; DOESBURG 1977; SCHUH & STYS 1991; SCHUH & SLATER 1995). So far the Vianaididae are known to contain five modern species belonging to two genera – *Anommatocoris* CHINA, 1945 (three species from Trinidad, Panama and Argentina) and *Thaumamannia* DRAKE & DAVIS, 1960 (two species from Bolivia and Surinam) and one fossil species (*Vianagramma goldmani* GOLUB & POPOV 2000) described from the Upper Cretaceous of North America (amber of New Jersey). A comparative analysis of morphological and some anatomic features of modern and, what is very important, of fossil Tingidae and Vianaididae made in our earlier papers allowed to prove that Vianaididae are an

independent family. There are also distinct autapomorphies for Tingidae and Vianaididae indicating that by the end of Mesozoic each family underwent long and independent evolution (GOLUB & POPOV 2000; GOLUB 2001).

This study presents results of our work on a fine collection of amber inclusions from the Late Cretaceous amber of New Jersey (Upper Turonian), from the American Museum of Natural History in New York (AMNH).

By some features, *Vianathauma*, n. gen. described herein, stands closer to recent forms than *Vianagramma* GOLUB & POPOV 2000. Moreover, a comparison of morphological features in fossil and modern Vianaididae helped to discover evolutionary tendencies that manifested themselves already in the Late Cretaceous while in the Cenozoic they led to the development of short-wing species with coleopteran forms of body and hemelytra as well as full-wing ones with areolate hemelytra and a characteristic appearance of tingoid Heteroptera.

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II. SYSTEMATIC PART

ORDER: HETEROPTERA

INFRAORDER: CIMICOMORPHA

Family: **Vianaididae** KORMILEV 1955

Family Vianaididae in: KORMILEV 1955: 466; MILLER 1971: 91; STYS & KERZHNER 1975: 72; KERZHNER 1981: 70; GOLUB, JOSIFOV, PERICART, KERZHNER, P. PUTSHKOV & V. PUTSHKOV 1996: 1; B. LIS 1999: 179; GOLUB & POPOV 2000: 242; GOLUB & POPOV 2001: 15, GOLUB 2001: 270.

Subfamily Vianaidinae in: DRAKE & DAVIS 1960: 8, 82, 84; DRAKE & RUHOFF 1965: 443; DOESBURG 1977: 185; SCHUH & STYS 1991: 327; SCHUH & SLATER 1995: 182.

Genus *Vianathauma* gen.nov.

D i a g n o s i s. Head, pronotum, and hemelytra without spines and tubercles. Head short and wide, not more than twice as wide as long and clearly wider than anterior margin of pronotum, without macrochetae. Ocelli present. Eyes large, strongly projecting on lateral sides of head. Proportions of antennomere length I-IV: I<II<III>IV; 1st antennal joint rather short yet reaching beyond apex of head, 2nd antennal joint 2 times longer than 1st and almost twice shorter than 3rd. Pronotum elongated, slightly shorter than wide, without areolate exposed cyst, longitudinal carinae, widened paranota and elongated posterior projection; anterior margin straight, lateral borders nearly concave, posterior margin emarginated arc-like. Scutellum completely exposed. External channels (grooves) of metapleural scent gland openings are Y-shaped (“ypsiform”). Macropterous form. Hemelytra weakly convex, divided only into corium and membrane, clavus not differentiated from corium. The latter not divided into areas by elevated longitudinal veins except feebly expressed costal (external) area. Hemelytral surface not areolate, only corium with rare and perforate-like punctation; membrane transparent and without veins.

Type species: *Vianathauma pericarti* sp. n., New Jersey amber, Upper Cretaceous.

E t y m o l o g y: refers to the family Vianaididae and genus *Thaumamannia*. Gender: feminine.

R e m a r k s. The new genus has two morphological features of the family that are characteristic of both modern genera, *Anommatoris* and *Taumamannia* and the other fossil genus of the family, *Vianagramma*: Y-shaped (“ypsiliform”) form of the peritreme of scent-gland openings and elongated antennal joint II which is longer than joint I. Besides that, the head of *Vianathauma*, the same as in all modern and fossil taxons of Vianaididae described earlier, is without spines which distinguishes this family from the representatives of the close family Tingidae. Similar to the other fossil genus *Vianagramma*, the genus described here has well developed hemelytra (*Vianagramma goldmani* is represented by the submacropterous form, *Vianathauma pericarti* – by the macropterous one) and normally developed compound eyes. Both species have large projections on the sides of head.

The new genus differs from the other Late Cretaceous genus *Vianagramma* mainly by following characters: 1) hemelytra surfaces without a complete cell structure, only with rare and large dots of punctation; 2) the membrane is completely transparent, without traces of cells; 3) except the costal field, the division of hemelytra by elevated longitudinal veins R+M and R+M+Cu into fields is absent: 4) ocelli present; 5) macrochaetae on the head absent.

In *Vianagramma* (Fig. 1), on the contrary, hemelytra have a complete small-cell structure of corium and clavus; corium is divided by longitudinal veins (probably, homologous to those of Tingidae) into costal, subcostal, and discoidal areas; and here the membrane along the outer margin has one row of very small, punctate-like cells, although almost everywhere else the surface is not areolate. There are macrochaetae on the head. Ocelli are absent. It is impossible to compare both taxa by the presence or absence of pulvilli (pseudoarollia) because of the cloud surrounding tarsi and their awkward position. There are also other, not so well expressed, differences between both Late Cretaceous genera as the length and thickness of antennal joints, head proportions and the degree of wing development.

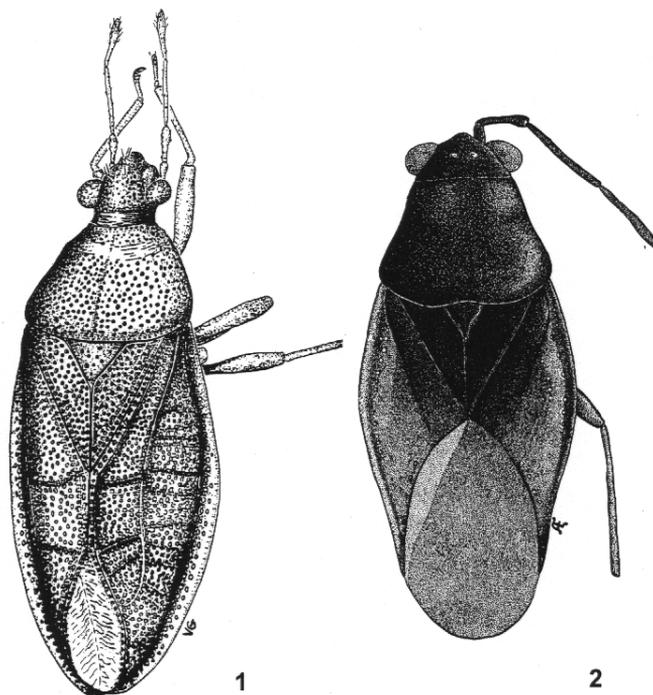


Fig. 1. *Vianagramma goldmani* GOLUB and POPOV; male holotype (Vianaididae; New Jersey amber, Upper Cretaceous).
Fig. 2. *Vianathauma pericarti* GOLUB and POPOV sp.n.; male holotype (Vianaididae; New Jersey amber, Upper Cretaceous).

Vianathauma pericarti sp.n.

(Figs 2-4)

Cimicomorpha, ? fam.nov.; male; no. NJ-37: GOLUB & POPOV, 2000: 232.

Vianathauma pericarti GOLUB & POPOV, 2001: 15-16 (Abstracts), (**nom. nud.**).

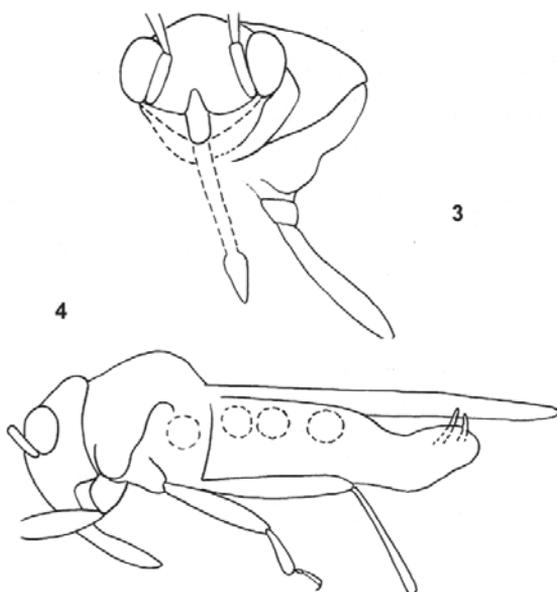
M a t e r i a l e x a m i n e d. Holotype: male from New Jersey amber (Upper Cretaceous), macropterous form, in AMNH coll., No. NJ – 37, New Jersey: Middlesex Co. Sayreville, White Oaks Pits; Aug.-Nov. 1993, coll. B. CORNET.

D e s c r i p t i o n. Body small, slightly longer than 2 mm, oblong-oval and flattened, 2.34 times longer than wide. Head and pronotum black; hemelytra extended far beyond tip of abdomen; fulvous, external parts of hemelytra along the whole side considerably lighter, brown. Surfaces of pronotum and hemelytra without hairs.

Head without spines, short and wide, 2.2 times wider than long and wider than anterior margin of pronotum; eyes large, semiglobular, strongly projecting on sides of head; ocelli present. Bucculae not protruding forward beyond apex of clypeus (we could not manage to determine whether bucculae are closed or open). Antennae brown, bare, rather long, with 2nd joint distinctly elongated and markedly thickened towards apex; twice longer than 1st (proportions of joints 1-4 are: 1:2:3.8:3.4; measurements are given below). Rostrum quite short not reaching posterior margin of metathorax. Number of tarsal joints and presence or absence of pulvilli not established.

Pronotum 1.2 times wider than long, its surface slightly punctate. Anterior margin straight, lateral borders of greater part of their length weakly emarginated, on the level of calli weakly projecting outside; paranota absent. Posterior margin of pronotum rounded and emarginated in middle. Scutellum completely exposed, small, triangular, apex pointed.

Macropterous form. Hemelytra extended far beyond tip of abdomen, without complete areolate structure, perforate-like punctation disposed mainly along inner margin of costal area in the form of a regular row. Lateral parts of corium not distinctly separated as costal area, without significant vein separating this area from other part of corium, which in its turn is not divided by elevated veins into areas.



Figs 3-4. *Vianathauma pericarti* GOLUB and POPOV sp.n.; holotype; 3 – head and pronotum, anteroventral view; 4 – lateral view.

Body black-brown ventrally. Peritreme of scent glands Y-shaped, which is not quite visible because ventral surface of thorax is covered with a milky film, preventing a closer study of morphological details.

M e a s u r e m e n t s (in mm). Body length (including hemelytra) 2.07, width 0.89; head: length 0.14, width 0.34; antennal joints: I: 0.1, II: 0.2, III: 0.38, IV: 0.34; pronotum: length 0.59, width 0.71 (max.); length of middle leg: femur 0.33, tibia 0.43; length of hind femur 0.49.

III. DISCUSSION

Trends in morphological evolution of Vianaididae

As shown earlier (POPOV 1989; GOLUB and POPOV 1999, 2000; GOLUB 2001), the oldest Tingoidea or their direct ancestors existed already in the Early Cretaceous. Two tribes are known from this time: Cantacaderinae (Tingidae) – Phatnomini and Golmoniini (POPOV 1989). Two genera described from imprints had already a main morphological feature of Tingoidea, i.e. areolation of surface (in both species very small and similar to punctation), and at least one of them, *Golmonia pater* POPOV, 1989, also had an elongated head similar to modern Cantacaderinae (FROESCHNER 1996). Undoubtedly the origin and initial stage of the super family evolution should be referred to the Early Cretaceous, possibly to its end (Aptian-Albian).

More recent fossil Tingidae are known only from the Late Eocene (Baltic amber). A study of the Eocene fauna of the family has shown its great diversity. Both recent subfamilies, Cantacaderinae and Tinginae are represented and the former also contains both modern tribes – Phatnomini and Cantacaderini. Judging from the quite developed features of both subfamilies and tribes of Cantacaderinae in the Late Eocene, the forming of the main features of the highest taxa of the family probably took place not later than the beginning or middle of Eocene or maybe still earlier. In both known Late Cretaceous genera of Vianaididae (*Vianagramma* and *Vianathauma*) the main features typical of the family (see above) were fully formed.

Analysis of morphological features of modern and fossil forms of superfamily Tingoidea (composed of Cantacaderini, Phatnomini, Tinginae, and Vianaididae) shows that this lineage is monophyletic (GOLUB 2001).

With some reservations, the following character states may be considered as unique synapomorphies for Tingidae and Vianaididae manifested by identical and clearly homological structures or tendencies pointed out earlier (DRAKE & DAVIS 1960; GOLUB & POPOV 2000; GOLUB 2001):

1. The areolate or at least partially punctate structure of hemelytra (except the greater part or the whole membrane in Vianaididae).
2. Division, or at least tendency towards division of hemelytra by elevated veins Hc, R+M, R+M+Cu into fields – costal, subcostal, discoidal, and sutural.
3. Flattened margins of pronotum – paranota in Tingidae and the tendency towards their formation in Vianaididae (*Vianagramma*).
4. The tendency, expressed to various degrees, to reduction of spermatheca; a synapomorphy known only in Recent forms.

The superfamily Tingoidea shares with a number of clearly non-relative families of Cimicomorpha other features: phytophagous type of rostrum and almost smooth surface of maxillae, the development of bucculae and disappearance of the hind bridge of tentorium, reduction of veins on the hemelytral membrane. These features are adaptative and developed independently in different families of Cimicomorpha; hence they are not synapomorphies (GOLUB 2001).

Each Tingoidea family manifests autapomorphies, which means that evolution of each of them was independent at least beginning with the middle of the Cretaceous (GOLUB and POPOV 2000; GOLUB 2001).

The main autapomorphies of Vianaididae are:

- 1) Y-like peritrema of the openings of scent glands;
- 2) considerably elongated 2nd joint of antennae;
- 3) absence of membrane venation;
- 4) head rather short

The above autapomorphies are observed already in the Late Cretaceous representatives of the family.

Vianaididae share common symplesiomorphic features with Cantacaderinae (GOLUB and POPOV 2000, GOLUB 2001): absence of posterior pronotal process, small cells of hemelytral corium and distinctly separated clavus, often with well expressed vein PCu (of Vianaididae only *Vianagramma* has the latter feature). These common features indicate that the above groups are older than Tinginae. And Vianaididae preserved more plesiomorphic features than Cantacaderinae: entire or almost entire membrane is not areolate (membranous), there are no spines on the head, at least in part of fossil specimens there were true setae-like pulvilli of tarsi and macrochetae on the head (GOLUB and POPOV 1999, 2000; GOLUB 2001). At the same time, if one considers simple (slot-like) peritrema of the openings of scent glands and the short II joint of antennae (shorter than joint I) as plesiomorphic features, then evolution of these structures in Vianaididae had to go at a greater speed than in Tingidae. In the latter, the plesiomorphic state of peritrema (the slot-like form) was preserved at least in the Eocene and probably later on in a number of genera and only in subfamily Tinginae (*Dictyla* STAL, 1874, and others) it disappeared for the second time. Proportions of two first antennal joints in all Tingidae remained unchanged from the beginning of their evolution.

Thus, as the analysis shows, formation of the main morphological features of Vianaididae by the end of the Mesozoic was almost completed, and new autapomorphies did not develop during their further evolution. In particular, in the Cenozoic the relative lengths of antennal joints and the form of peritrema of scent gland openings did not undergo any changes at all. In the Cenozoic, there appeared only adaptations and features that pointed to reduction of individual morphological structures (see below) due to the transfer of at least part of species to myrmecophilia and the cryptic way of life. Taking into account the historical age of fossil Vianaididae and the level of formation of the above syn- and autapomorphies, the time of the final formation of family Vianaididae should probably be defined as the middle or beginning of the second half of the Cretaceous.

It is well known (DRAKE and DAVIS 1960; DRAKE and RUHOFF 1965) that all the five modern brachypterous species of Vianaididae leading cryptic way of life have a coleopteroid form of body, shortened punctate hemelytra without membrane, and areolation of body surface characteristic of most Tingoidea (DRAKE and DAVIS 1960). Their faceted eyes are greatly reduced. Yet also macropterous modern Vianaididae are known, although not yet described, with normally developed compound eyes and areolate structure of body surface. They preserved a number of initial morphological features (SCHUH and STYS 1991; SCHUH and SLATER 1995).

Thus, in modern Vianaididae, one can observe a distinct differentiation into forms with features characteristic of Tingoidea and those with expressed features of specialization and reduction of individual organs. Hence a question arises – in which stage of evolution Vianaididae began to manifest the features of their morphological differentiation and divergence with separation of cryptic forms? What preadaptive features could form the basis of the morphological specialization associated with myrmecophilia?

Fossil forms of Vianaididae do not yet show a distinct morphological specialization. Nevertheless, in the structure of body surface, which is the characteristic morphological feature of Tingoidea, divergence is evident already in the Late Cretaceous. Two representatives – *Vianagramma goldmani* (Fig. 1) and *Vianathauma pericarti* (Fig. 2), demonstrate this. And the diverging forms have a mosaic composition of plesiomorphic and apomorphic features. The first trend in the evolution represents a phylogenetic branch that comprises non-specialized forms of the family that changed little from the end of the Mesozoic.

The other evolutionary line that in the Cenozoic brought about cryptic myrmecophilous species should probably be associated with preadaptive features that in *V. pericarti* appeared already in the Mesozoic. All the modern species of this group known so far have a coleopteran body and non-areolate but only punctate hemelytra with their borders fused and undivided by longitudinal veins into fields. Facetted eyes are greatly or completely reduced.

In the Mesozoic *Vianathauma* plesiomorphic features of hemelytra – absence of areolation and division by longitudinal veins into areas – can be easily observed. Here the costal area is not quite distinct and is not separated from the rest of corium by Hc vein. A rather large and sparse punctuation of hemelytra in *V. pericarti* is probably an initial feature. The secondary development of punctuation out of areolation already in the Mesozoic is less probable. Absence of areolate structure in transparent membrane and normally developed, facetted eyes are symplesiomorphies with *V. goldmani*. However, absence of venation in the membrane (feature synapomorphic with *Vianagramma*) points to the process that began already in the Mesozoic. The extended lateral margin of hemelytra in the form of a plate is possibly homologous to the costal area of *Vianagramma* and to all Tingidae. It is very similar with the analogous structure of the hemelytra of modern *Thaumamannia manni* and probably represents by itself apomorphy as well (possibly a synapomorphy with *Vianagramma* and Tingidae). The presence of ocelli should also be considered as plesiomorphy.

As a whole, besides the above autapomorphies of all Vianaididae (synapomorphies with *Vianagramma*), the only proved autapomorphic feature of *Vianathauma* is probably the absence of macrochetæ on the head. Having changed to cryptic way of life, this phylogenetic branch originating from the forms without an areolate structure of hemelytra yet with punctuation alone (*Vianathauma* is such a representative), could give the beginning to the modern short-wing coleopteran forms with more or less well-developed punctuation of hemelytra.

Thus, already at the end of the Mesozoic and during the Cenozoic, two directions of evolution of Vianaididae became evident. One of them, originating from the forms with well developed hemelytra cells and hemelytra divided like in Tingoidea (*Vianagramma*), led to preservation of synapomorphies typical of Tingidae.

Representatives of the other direction, with a greater set of plesiomorphic features, in particular without developed cells of hemelytra (*Vianathauma*), turned out to be better adapted to life in ant nests (probably myrmecophilous inquilines). The reduction of facetted eyes and membrane as well as development of a coleopteran form of body undoubtedly took place already in the Cenozoic. And this reconstruction of the exterior organization of myrmecophilous Vianaididae could take place simultaneously with the evolution of Formicidae.

In particular, besides the presence of synapomorphies with *Vianathauma* (see above), *Vianagramma* is characterized by such unique plesiomorphic features as macrochetæ on the head and, probably, true pulvilli. And here quite distinct are such apomorphic (synapomorphic with Tingidae) features as the division of hemelytra by longitudinal veins (evidently, homologous to those of Tingidae Hc, R+M, R+M+Cu) into areas (costal, subcostal, discoidal, sutural) and the areolate structure of the covers of corium and clavus (small, punctuation-like) in combination with rather a large punctuation of the pronotum disc. Moreover, despite the fact that almost all membrane of this species is not areolate (plesiomorphy), on its exterior margin there is a row of very small, punctuation-like cells (apomorphy).

However, it should be noted that the areolation of hemelytra of the Late Cretaceous *Vianagramma* may be considered as synapomorphy only in respect to Tingidae as a whole and without account of the size of cells. Yet, when considering their small size, this feature should be looked upon as a symplesiomorphic feature with Cantacaderinae, whose most species have body surfaces with tiny cells. The small areolate structure of corium and the non-areolate structure of *V. goldmani* membrane – these are the features that probably reflect one of the initial stages in the evolution of the areolate structure of all Tingoidea. Having developed as a structure of corium (most probably of punctuation), later on the areolation could spread over to membrane and with the appearance of paranaota and the posterior pronotal projection (in Tinginae) – over them. The absence of ocelli could

also be considered as an autapomorphic feature of *V. goldmani* and the presence, although sparse, of medial carina of pronotum – as synapomorphy with Tingidae.

Thus, the Late Cretaceous species *V. goldmani* with its areolate structure of body surface stands closer to Tingidae exhibiting synapomorphic features of both families as well as some symplesiomorphic features with Cantacaderinae. Further evolution of the forms of *V. goldmani* type with an areolate structure of hemelytra has probably led to the development of a group of known but not yet described modern full-wing species Vianaididae with areolate structure.

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